



Seagrass response following exposure to *Deepwater Horizon* oil in the Chandeleur Islands, Louisiana (USA)

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ABSTRACT: The Chandeleur Islands, Louisiana (USA), were among the first coastal locations in the northern Gulf of Mexico (GoM) threatened by exposure to *Deepwater Horizon* oil. Shoreline oiling data and surface oil trajectories (aerial and satellite imagery) showed oil passing through seagrass beds on the shallow back barrier shelf west of the islands repeatedly between May and early July 2010. Aerial photos in May 2010 revealed a heterogeneous distribution of surface oil crossing the shelf, and MC252 exposure was confirmed in sediments and seagrass tissue during field assessments. We observed 5 seagrasses growing at densities comparable to other northern GoM communities. *Ruppia maritima* and *Halodule wrightii* were the most common, followed by *Thalassia testudinum*. *Syringodium filiforme* and *Halophila engelmannii* were rarely encountered. The subtidal and intertidal seascape on the shelf was a mosaic of seagrass patches distributed in varying sizes among unvegetated and sparsely vegetated areas at water depths and in sediment types known to support seagrasses. To quantitatively assess the seagrass response following exposure, sophisticated change detection methodologies were applied to aerial photography acquired in October 2010, 2011, and 2012 in a subsample of 5 locations on the shelf where *Deepwater Horizon* oil exposure was confirmed. The analysis conservatively estimated a seagrass loss of 104.22 acres (42.18 ha) at these locations. Unexpectedly, the whole back barrier shelf experienced a net gain of 228 acres (92.27 ha) of seagrass between 2010 and 2011, representing a pause in the long-standing trend in seagrass declines in the Chandeleurs and indicating that oil exposure did not result in a shelf-wide catastrophe for seagrasses. Predictions for the impending disappearance of this seagrass resource in the near future may need to be reconsidered.

KEY WORDS: Oil spill · Gulf of Mexico · Seagrass communities · Change detection

INTRODUCTION

The shallow coastal waters of the northern Gulf of Mexico (GoM) are ecologically important habitats for fish, shellfish, and wildlife that provide highly valued recreational, economic, and aesthetic services to society. Seagrasses are among several coastal habitats

that contribute to attaining these values by providing a wide range of ecological services (Michot & Chadwick 1994, Beck et al. 2001, Duarte et al. 2005, Larkum et al. 2006, Orth et al. 2006b, Waycott et al. 2009, Barbier et al. 2011). In the northern GoM, 6 seagrass species are widely distributed along the coastlines in lagoons, bays, and barrier islands from

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§Advance View was available online February 7, 2017

§§Corrections were made after publication. For details see www.int-res.com/abstracts/meps/v576/c_p145-161/
This corrected version: August 7, 2017

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Publisher: Inter-Research · www.int-res.com

Texas to the panhandle region of northwest Florida (Green & Short 2003, Handley et al. 2007, Ray et al. 2014). They grow in water depths ranging from the intertidal to 10 m, but water clarity generally limits their growth to ≤ 2.0 m in nearshore waters, making them especially vulnerable to anthropogenic disturbances, including degraded environmental quality (Orth et al. 2006b, Waycott et al. 2009) and exposure to oil (Zieman et al. 1984). Seagrasses are considered 'ecological engineers' (van der Heide et al. 2012) because their leaf canopies baffle water flow and wave energy, and belowground rhizome and root structures bind and stabilize substrates (Fonseca et al. 1983, Fonseca & Bell 1998, Duarte & Chiscano 1999). These attributes promote the deposition and retention of sediments, organic matter, and other materials within the meadows and are widely cited as some of the major functions of seagrass beds (Larkum et al. 2006). However, these important functions may also be an 'Achilles heel' in an oil spill. In shallow water and intertidal areas, seagrass canopies can extend well up into the water column, sometimes even to the water surface, where they can come into direct contact with oil, weathered petroleum, and dispersants during a spill. At the same time, sea-

grasses can promote the deposition of contaminants associated with suspended sediments and organic matter. Once these contaminated materials are deposited, they are not easily resuspended or transported out of the meadows, and are likely to be retained and concentrated in the leaf canopy and sediments where important bio-physical processes can become exposed to toxic chemicals.

Following the *Deepwater Horizon* (DWH) explosion on 20 April 2010, Macondo oil from the Mississippi Canyon Block 252 (MC252) traveled upward from the wellhead through the 1.5 km water column to form expansive surface oil slicks which were transported to nearshore coastal ecosystems by wind and currents (Peterson et al. 2012). Synthetic Aperture Radar (SAR) detection of surface oil (Graettinger et al. 2015) and shoreline surveys (Michel et al. 2013) demonstrated light to heavy oiling events in nearshore environments as far west as Atchafalaya Bay, Louisiana (LA), and as far east as Apalachicola, Florida (FL) (Fig. 1). Some shorelines were repeatedly oiled during the spill and long after the wellhead was capped, as early as 3 May 2010 (Michel et al. 2013) and as late as 26 July 2010 (<http://gomex.erma.noaa.gov/erma.html>; Daily Integrated Oil Cover).

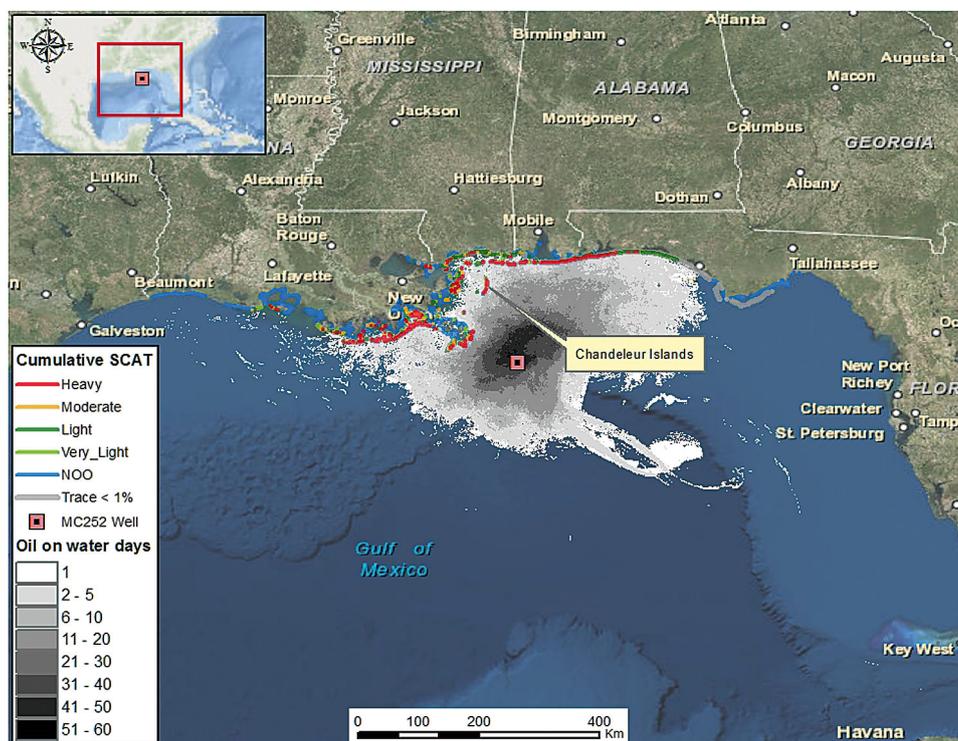


Fig. 1. Location of the Chaudetour Islands, Louisiana, USA, in the northern Gulf of Mexico (29.84° N, 88.84° W), showing the estimated number of days that oil (MC252) from the *Deepwater Horizon* spill remained on the water surface (based on Synthetic Aperture Radar satellite imagery) and extent of cumulative shoreline oiling (assessed by the Shoreline Cleanup Assessment Technique, SCAT). NOO: no oil

In early May 2010, oil began reaching ecologically sensitive shallow coastal habitats in the northern GoM known to have seagrasses, including the offshore barrier islands of LA (Handley et al. 2007) (Fig. 1).

The Chandeleur Islands, LA, were among the earliest locations where seagrass meadows were oiled. Evidence based on direct observations of shoreline oiling by the Shoreline Cleanup Assessment Technique (SCAT) in early May 2010 (Michel et al. 2013) confirmed oiling along a large portion of the western shoreline and fringing marshes of the Chandeleurs (Fig. 2). Oiling of the Chandeleur Islands was confirmed by SCAT surveys as early as 8 May 2010, and oil on water was clearly visible in imagery from the National Agriculture Imagery Program (NAIP) from 10 May 2010 (Fig. 3). Light to heavy oiling was

identified throughout the islands during SCAT surveys conducted from 21 through 28 June and when SCAT teams returned to the Islands from 11 through 13 July (see SCAT survey data from <http://response.restoration.noaa.gov/erma/> - 27 September 2014 Cumulative Oiling Ground Observations).

Several direct impacts of oil and dispersants on seagrasses have been documented, ranging from complete mortality (Foster et al. 1971a,b, Zieman et al. 1984, Thorhaug & Marcus 1987, Jackson et al. 1989, Sandulli et al. 1998, Scarlett et al. 2005) to leaf exfoliation, sublethal stress and chronic impairment of seagrass and sediment metabolism and function (Hatcher & Larkum 1982, Ralph & Burchett 1998, Peirano et al. 2005) (see Supplement 1 at www.int-res.com/articles/suppl/m576p145_supp.pdf). Sec-

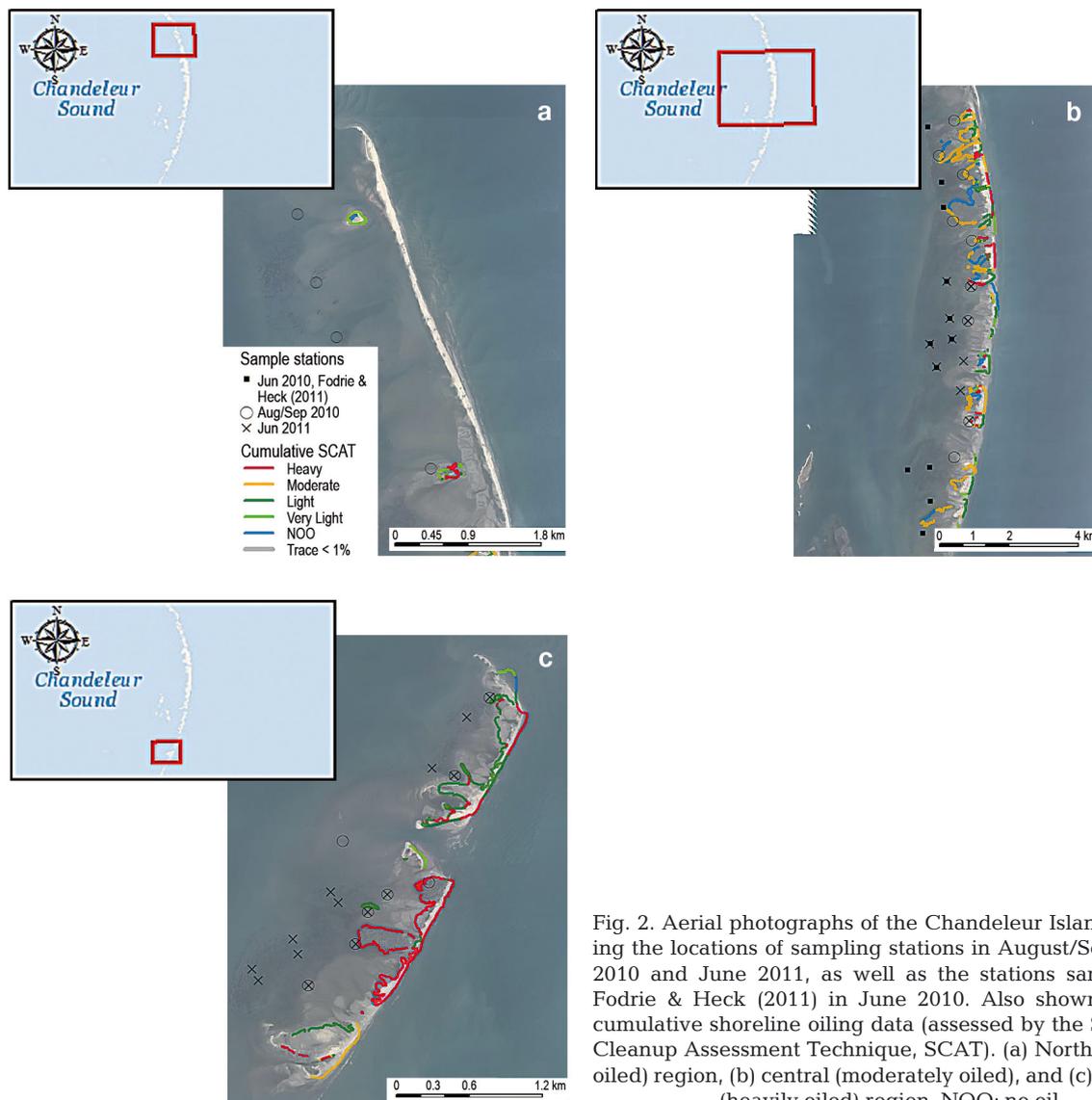


Fig. 2. Aerial photographs of the Chandeleur Islands showing the locations of sampling stations in August/September 2010 and June 2011, as well as the stations sampled by Fodrie & Heck (2011) in June 2010. Also shown are the cumulative shoreline oiling data (assessed by the Shoreline Cleanup Assessment Technique, SCAT). (a) Northern (non-oiled) region, (b) central (moderately oiled), and (c) southern (heavily oiled) region. NOO: no oil

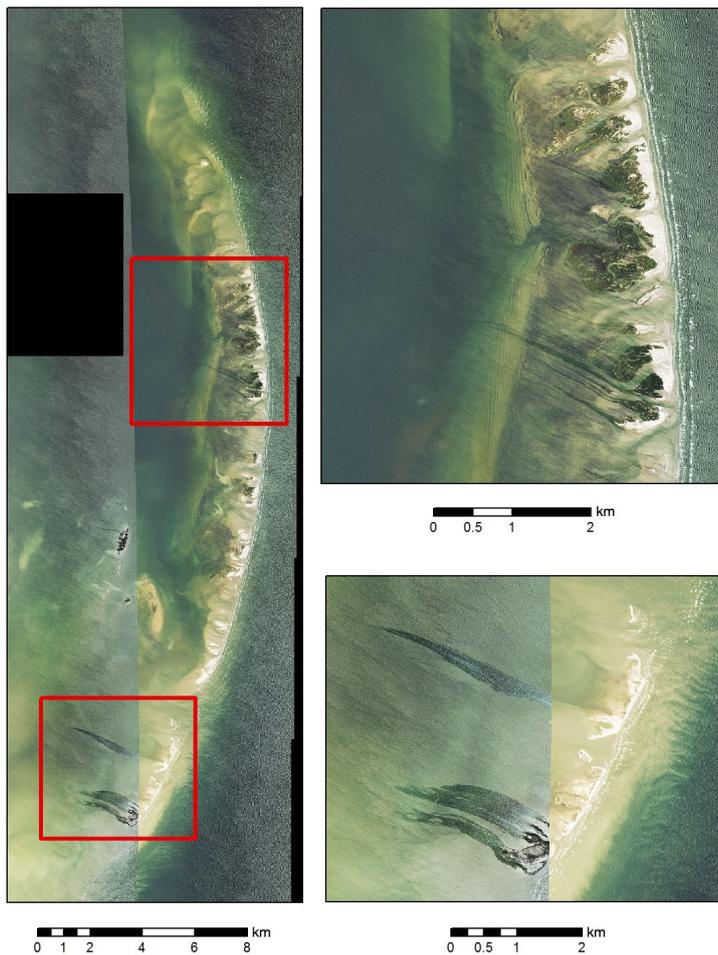


Fig. 3. National Agriculture Inventory Program (NAIP) aerial photographs taken in May 2010 showing surface sheens of oil on water in the central and southern regions of the Chandeleur Islands. Areas in the red squares are enlarged in the panels to the right

ondary impacts also include biophysical and chemical disturbance to sediments, microbes, microfauna, and microflora, epiphytes, and the impairment and mortality of secondary producers residing in the seagrass canopy and sediments (e.g. invertebrates, crustaceans, fishes, waterfowl) (Diaz-Piferrer 1962, Tatem et al. 1978, den Hartog & Jacobs 1980, Carls & Meador 2009). Response actions and cleanup efforts in seagrass beds and adjacent shorelines can also cause environmental degradation and seagrass loss (Zieman et al. 1984, NOAA 2011). In several field assessments following oil spills, the most severe impacts to seagrasses were documented in shallow subtidal and intertidal habitats where petroleum and weathered byproducts came into prolonged direct contact with seagrasses, fauna, other flora, and sediments. Generally, there is agreement that deeper subtidal meadows are less vulnerable to exposure (Zie-

man et al. 1984, Durako et al. 1993), and the potential impacts of oil depend on the unique bio-physical characteristics of a site, such as distance from the source, weathering, tidal range, water depth, wind and wave exposure, currents, substrate type, and species composition (Zieman et al. 1984, Kenworthy et al. 1993, Hayes et al. 1993).

Given the wide range of potential impacts of oiling on seagrasses and the documentation of *Deepwater Horizon* oiling in shallow waters and shorelines of the Chandeleurs, the objectives of this study were (1) to determine the degree and extent of *Deepwater Horizon* oil exposure in seagrass meadows at the Chandeleur Islands, (2) characterize the communities of seagrasses exposed, and (3) quantitatively assess the distribution and abundance of seagrasses following the exposure.

MATERIALS AND METHODS

Study site

The Chandeleurs are a north–south oriented chain of narrow, arcuate, transgressive barrier islands slightly elevated above sea level and located ~50 km south of Gulfport, Mississippi, and 125 km north of the *Deepwater Horizon* oil well (Fig. 1). Seagrass meadows occur on a shallow shelf extending 1 to 2 km westward of the islands to a slightly elevated subtidal back barrier bar where the shelf terminates in the relatively deeper water of Chandeleur Sound (Poirrier & Handley 2007, Pham et al. 2014). The islands deflect wind, wave, and current energy from the open GoM, making the western fringing shelf a semi-protected lagoon-like environment with shallow water (≤ 2.0 m) well within the photic zone and physically ideal for seagrasses to thrive.

General sampling design and chronology

Initial exposure sampling (June 2010)

Sediment and plant samples were collected opportunistically in conjunction with an ongoing project designed to sample 12 locations with seagrasses in the Chandeleur Islands (Fodrie & Heck 2011; Fig. 2).

Despite initial efforts to conduct pre-spill sampling of ambient conditions, we were unable to acquire samples at the Chandeleur Islands until 2 June 2010; therefore, pre-exposure ambient concentrations of oil-related compounds at the Chandeleur Islands could not be confirmed.

Post-spill exposure sampling (August–September 2010)

Initially, the SCAT data were used to qualitatively establish a preliminary stratification of the Chandeleur Islands into (1) heavy oiling (southern region), (2) moderate oiling (central region), and (3) no oiling (northern region) and were incorporated into field sampling plans between 31 August and 2 September 2010 (Fig. 2). The sampling plan relied on the best available knowledge of seagrass presence/absence based on prior mapping studies (Handley et al. 2007) and knowledge of the proximity of known seagrass beds to oiled shorelines determined by SCAT surveys. For initial selection of sampling stations, post-Hurricane Katrina seagrass survey data from the coast of Mississippi and Alabama (Byron & Heck 2006) were used to help determine sampling density for small, discontinuous submerged aquatic vegetation (SAV) beds in the northern GoM. Statistical analysis of these data determined that a distance of 400 m between sample stations was required to meet the following decision parameters: Type I error or α (erroneously declaring a site non-impacted) = 5% (significance or confidence = 95%); Type II error or β (erroneously declaring a site impacted) = 10%, or a test power of 90% to correctly reject the null hypothesis; and test resolution or Δ , which is the percent change in mean value detected at 95% confidence. Additionally, a target distance of approximately 500 m between stations was determined sufficient to detect the desired percent change in observed SAV conditions at a site relative to those observed at a comparable reference site with 95% confidence (Type I error = 5%) and 90% statistical test power (Type II error = 10%).

Post-spill exposure sampling (June 2011)

Based on further inspection of SCAT data, surface oiling in NAIP aerial imagery, and laboratory screening of the initial exposure samples obtained in 2010, the preliminary stratification of oiling categories were modified in June 2011 to include only the cen-

tral and southern regions of the Chandeleurs with the addition of more sampling stations to gain wider spatial coverage across the shelf (Fig. 2b,c). Several stations from 2010 were also resampled to determine persistence of exposure over time.

Oil exposure sampling methods and analyses

Sediment samples

Samples were collected in the top 2 cm of the sediment and subjected to laboratory analysis for total polycyclic aromatic hydrocarbon (tPAH) surrogate-corrected concentrations, calculated based on the summation of 54 PAH analytes including parent PAHs and selected alkylated homologs listed in Forth et al. (2015) (see Supplement 2 at www.int-res.com/articles/suppl/m576p145_supp.pdf for a list of PAHs). If the concentration of a given compound in a sample was not detected, it was treated as a 0 value in the summation. Two other PAH sums were also used to help distinguish types of PAHs: (1) PAHs associated with petroleum, like oil from the DWH spill (petrogenic) and (2) PAHs associated with the partial combustion or pyrolysis of organic matter (pyrogenic) (Emsbo-Mattingly & Martin 2015).

PAHs, including alkyl homologues, were analyzed in compliance with modified US Environmental Protection Agency method 8270 (US EPA 2015), utilizing gas chromatography with low-resolution mass spectrometry in the selected ion monitoring mode. The analytical chemistry results were subjected to rigorous quality assurance/quality control and validation procedures, as described in the NRDA Analytical Quality Assurance Plan (NOAA 2014) and Data Validation Plan (EcoChem 2011), respectively.

Seagrass tissue

Plant tissue samples identified as leaves and stems were obtained from the seagrass meadow canopy and sub-sampled twice in the laboratory. One sub-sample, referred to as 'external materials,' included only epiphytes and inorganic material loosely adhered to the leaves. This material was gently washed from the leaves and rinsed with dichloromethane, and the resulting rinsate was dried and measured for PAHs. The other sub-sample was rinsed with deionized water and homogenized before analysis. PAHs were analyzed as described above for the sediment samples.

Confirmation of oiling using SAR data

SAR identifies very thin surface oil slicks by detecting a change in backscatter resulting from oil-dampening surface capillary waves (Graettinger et al. 2015). SAR data were collected, compiled, and analyzed from 25 April to 26 July 2010, and an estimate of cumulative oiling per 50 m × 50 m grid area was calculated by adding overlapping grid cells to determine total oiled days. In order to calculate the average oil on water days for a particular site, seagrass polygonal areas delineated using fall 2010 aerial imagery (see Fig. 5) were spatially joined to the cumulative oiling raster grid dataset in ArcGIS software (Fig. 4). Each seagrass area less than 2500 m² was associated with the closest 2500 m² grid estimate, while larger seagrass areas were assigned the average oil on water days for encompassed grid cells. Finally, a spatially-weighted average number of oil on water days was calculated for the Chandeleur Islands.

Characterization of Chandeleur Island seagrasses

Post-exposure sampling (August/September 2010)

Initially, the selection of sample sites was guided by the criteria described above. Seagrass characteri-

zation and exposure sampling were conducted at the same stations: (1) no oiling in the northern region (n = 4), (2) moderate oiling in the central region (n = 9), and (3) heavy oiling in the southern region (n = 8), for a total of 21 stations (Fig. 2).

Field assessments of the cover, abundance, and general condition of seagrass beds in the Chandeleur Islands were conducted between 21 August and 2 September 2010, almost 4 mo after initial oiling. Field teams navigated to pre-determined geographic coordinates and verified the presence or absence of seagrass. If seagrass was absent, snorkelers conducted systematic circle searches until seagrass was located, at which time the alternate waypoint was stored in the GPS as the final sampling location.

The species composition and percent cover of seagrass at each station was estimated using a modified Braun-Blanquet visual assessment technique averaged from 0.25 m² PVC quadrats (n = 3) haphazardly tossed into the seagrass bed (Braun-Blanquet 1932, Kenworthy et al. 1993, Fourqurean et al. 2001). Additionally, 3 plant/sediment cores (15 cm diameter) were collected to estimate shoot density of individual species. During all sampling, observers noted if oil was present on the seagrass or sediments and made qualitative observations of oiling and the health and condition of leaves, whole shoots, rhizomes, roots, apical meristems, new shoot and rhizome growth, and epiphytes.

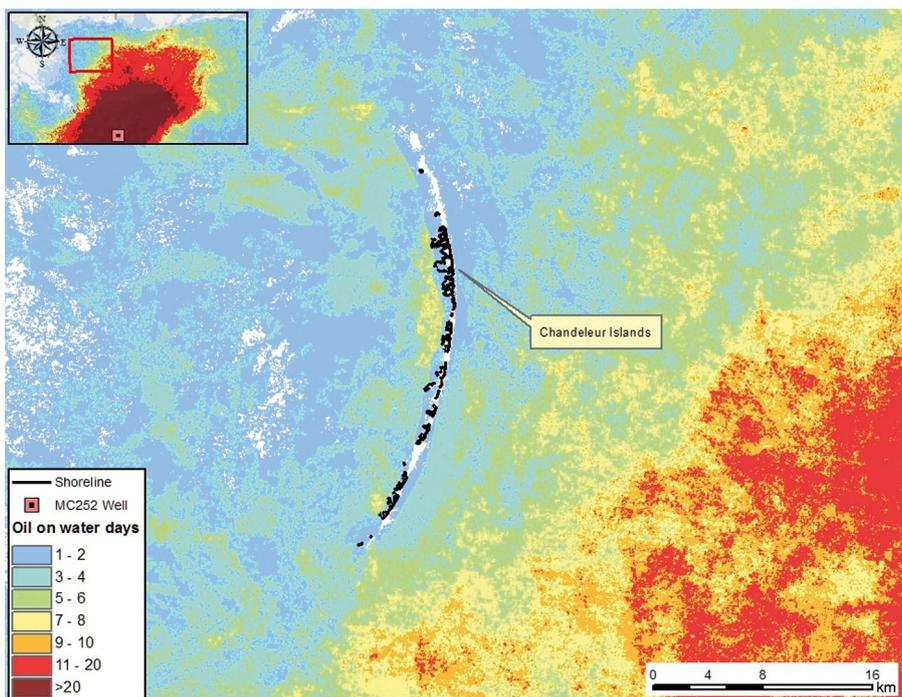


Fig. 4. Estimated number of days that oil from the *Deepwater Horizon* spill remained on the water surface at the Chandeleur Islands (based on Synthetic Aperture Radar satellite imagery)

Post-exposure sampling (June 2011)

Field assessments and sample processing (20 to 22 June 2011) followed the same general protocols as in September 2010 with 3 exceptions: (1) the original oiling stratification categories were modified to focus only on the central region (formerly referred to as moderately oiled; $n = 10$) and southern region (formerly referred to as heavily oiled; $n = 14$; Fig. 2b,c); (2) sampling intensity was increased to 5 quadrats and 5 cores within each stratum; and (3) inshore, mid-shore, and offshore stations were sampled to gain more comprehensive shelf-wide information about the seagrass beds.

Aerial imagery interpretation, seagrass mapping, and change analysis

A hybrid imagery analysis technique incorporating automated object-based imagery analysis (OBIA) (Benz et al. 2004) and traditional photo-interpretation methods (Handley et al. 2007) was used to map the presence/absence of seagrasses in high-resolution aerial imagery acquired on 3 dates in the fall of 2010, 2011, and 2012 (Fig. 5) (Handley et al. 2010, NOAA 2013). Specific additional details on the hybrid method are provided in Supplement 3 at www.int-res.com/articles/suppl/m576p145_supp.pdf. Fall imagery was the first available opportunity and coinci-

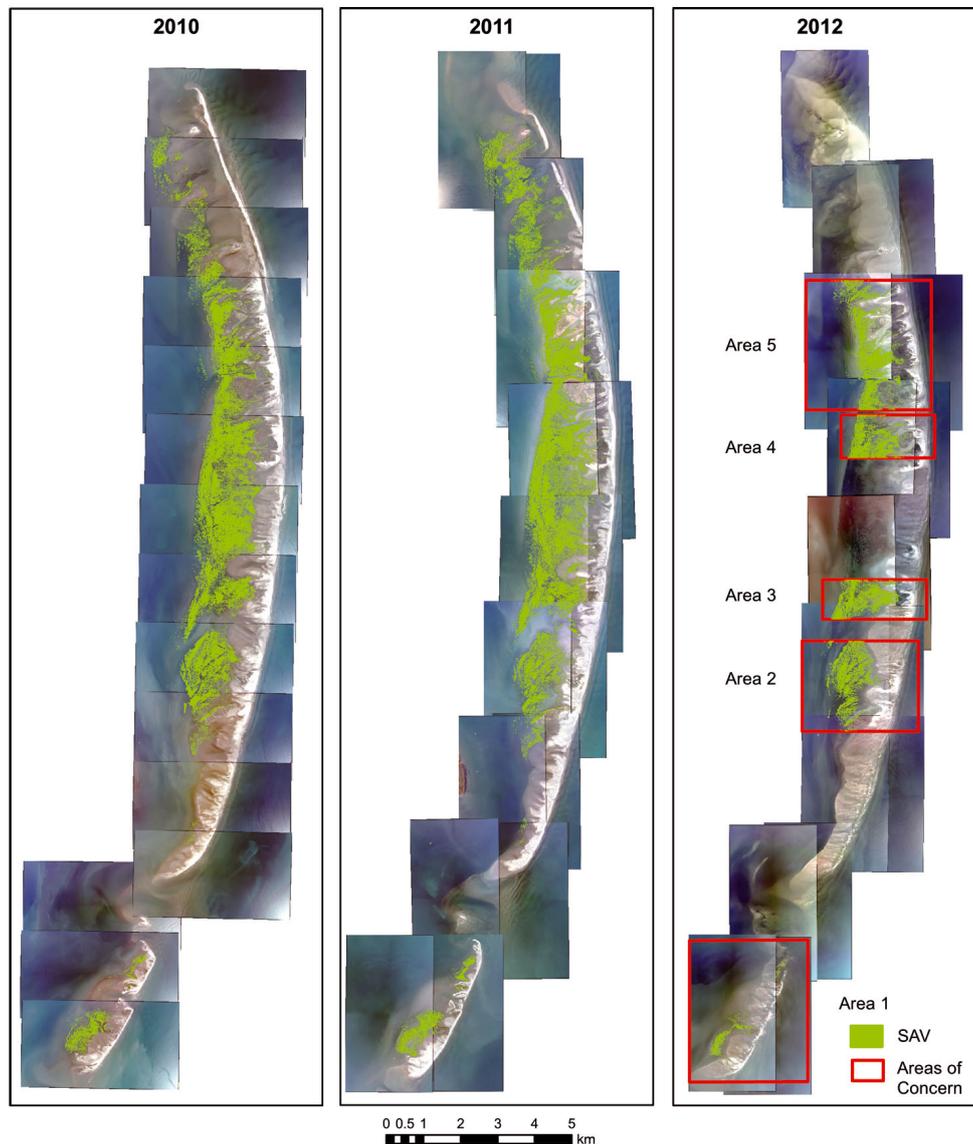


Fig. 5. High-resolution aerial photograph and interpreted classification of seagrass (submerged aquatic vegetation, SAV) presence (green areas) for 3 years (October 2010, 2011 and 2012). Also shown highlighted in the red polygons are the 5 areas of concern where detailed change analyses were conducted

dently the preferred signature index period, since the meadows were expected to be at their maximum extent and biomass. There was no reliable source of pre-spill imagery, so October 2010 imagery was considered baseline for the analysis. The 12-bit imagery, with a pixel resolution of 0.3 m, was collected using multiple DMS sensors and met ASPRS Class 2, 1:24 000 scale accuracy standards, which limit the RMS error in x or y to 1.2 m. Complementary ground truth information on seagrass distribution, abundance, and species composition were obtained during field sampling at the Chandeleur Islands on 2 June 2010 (Fodrie & Heck 2011), between 31 August and 2 September 2010, and again between 20 and 22 June 2011.

The mapping and change analysis classification scheme was binary (presence/absence of seagrass), consisting of 2 classes: seagrass (SAV) and not seagrass (NOT SAV). Although the classification scheme was binary, samples of many other features were identified in order to be removed from consideration as seagrass, and these consisted primarily of sand substrates and other non-seagrass features (e.g. detritus). The change detection analysis consisted of 2 parts: (1) change between 2010 and 2011 along the full length of the Chandeleur Islands, and (2) change between all 3 dates of mapping (2010, 2011, and 2012) within 5 areas of concern (AOCs) identified within the Chandeleur Islands based on plumes of surface oil observed in NAIP imagery (10 May 2010; Fig. 3) in combination with SCAT information (Fig. 2) and field data indicating exposure to MC252 oil (see 'Results').

Since the objective of the change detection was to identify areas of seagrass loss corresponding with documented oil exposure, we refined the analysis to discriminate between natural losses and those potentially related to oil exposure. 'Core areas' were identified and delineated within each of the AOCs (see Supplements 3 & 4 at www.int-res.com/articles/suppl/m576p145_supp.pdf). Core areas represent areas where imagery interpretation could not be attributed to seagrass losses due to natural processes between 2010 and 2012.

RESULTS

tPAH exposure

Sediments

The highest tPAH concentrations, 312 ± 184 ppb (mean \pm SE), were recorded during sampling between 31 August and 2 September 2010 when values were nearly 8 times higher than initially observed on 2 June 2010 (40.8 ± 9.1 ppb; Table 1). Likewise, the maximum recorded value in the August/September samples was also demonstrably higher (3998 ppb) than the maximum in June (105 ppb). Concentrations of petrogenic PAHs followed the same temporal pattern, with higher values in August/September (285 ± 171 ; max = 3713 ppb) than first recorded in June (27.0 ± 6.1 ppb; Max = 75.4 ppb) (Table 1). In June 2011, approximately 1 yr after initial oiling occurred, sediment tPAHs (69.7 ± 9.9 ppb) and petrogenic PAHs (50.7 ± 9.1 ppb) had both declined, but were still higher than values recorded initially in June 2010 (Table 1).

Plant tissue

As was the case for sediments, concentrations of tPAHs were higher in August/September 2010 (44.2 ± 12.4 ppb) than in June 2010 (3.5 ± 0.5 ppb) (Table 2). Likewise, maximum tPAHs (264 ppb) in August/September 2010 were 35 times higher than in June (7.4 ppb). The petrogenic PAH mean (38.0 ± 11.1 ppb) was also higher in August/September than recorded in June (1.4 ± 0.3 ppb) and declined 1 yr later, in June 2011 (8.2 ± 4.5 ppb).

External materials

High concentrations of tPAHs were recorded in the external materials rinsed from the seagrass leaves

Table 1. Summary of mean (\pm SE) total polycyclic aromatic hydrocarbons (tPAH) and petrogenic (PET) and pyrogenic (PYR) PAH concentrations in sediments at the Chandeleur Islands, Louisiana, on 3 sampling dates (given as mm/dd/yyyy). Also shown are the maximum (max) values for each and the number of samples (N). All results are in parts per billion (ppb)

Sampling date	N	Mean tPAH	tPAH max	Mean PET PAH	PET PAH max	Mean PYR PAH	PYR PET max
06/02/2010	12	40.8 ± 9.1	105	27.0 ± 6.1	75.4	13.6 ± 3.1	30.0
08/31–09/02/2010	22	312 ± 184	3998	285 ± 171	3713	26.3 ± 12.8	283
06/20–06/22/2011	52	69.7 ± 9.9	425	50.7 ± 9.1	395	19.0 ± 2.1	91.9

Table 2. Summary of mean (\pm SE) total polycyclic aromatic hydrocarbons (tPAH), petrogenic (PET), and pyrogenic (PYR) PAH concentrations in 2 sample types: plant tissue (Plant) and external material rinsed from plant tissue (EM) at the Chandeleur Islands, Louisiana, on 3 sampling dates (given as mm/dd/yyyy). Also shown are the maximum (max) values for each and the number of samples (N). All results are in parts per billion (ppb)

Type	Sampling date	N	Mean tPAH	tPAH max	Mean PET PAH	PET PAH max	Mean PYR PAH	PYR PET max
EM	06/02/2010	12	67239 \pm 42789	535598	28710 \pm 16590	208300	38524 \pm 26339	327298
Plant	06/02/2010	12	3.5 \pm 0.5	7.40	1.4 \pm 0.3	2.91	1.9 \pm 0.3	4.09
EM	08/31–09/02 2010	21	174217 \pm 75929	1661945	139890 \pm 70934	1541760	34224 \pm 8460	148970
Plant	08/31–09/02 2010	21	44.2 \pm 12.4	264	38.0 \pm 11.1	234.2	6.2 \pm 1.4	29.9
EM	06/20–06/22 2011	24	47417 \pm 22827	569786	38532 \pm 22277	526910	10974 \pm 2225	42876
Plant	06/20–06/22 2011	26	10.0 \pm 5.0	132	8.2 \pm 4.5	120	1.9 \pm 0.5	12.1

(Table 2). As was the case for both plant tissue and sediments, the highest concentrations were recorded in the August/September sampling (174 217 \pm 75 929 ppb) and were 2.6 times greater than in June 2010 (67 239 \pm 42 789 ppb). By June 2011, the tPAH concentration had declined (47 417 \pm 22 827 ppb) and was less than the value recorded 1 yr earlier. Maximum tPAH values followed the same temporal pattern as did petrogenic PAHs, which were nearly 5 times higher in August/September 2010 (139 890 \pm 70 934 ppb) than in June 2010 (28 710 \pm 16 590 ppb) and declined to 8.2 \pm 4.5 ppb in June 2011.

Seagrass distribution, species composition, and abundance

August/September 2010

In late August 2010, approximately 3 mo after *Deep-water Horizon* oil first arrived at the Chandeleur Islands, the spatial distribution of seagrasses on the shallow shelf west of the islands was discontinuous (Fig. 5). The subtidal and intertidal landscape consisted of a mosaic of seagrass patches distributed in varying sizes among areas of unvegetated and sparsely vegetated bottom. Generally, meadows in the vicinity of the central region of the islands were larger and relatively more continuous than the meadows in the northern and southern regions, which were more fragmented.

Five of the 6 species of seagrass known to occur in the northern GoM were observed, but only 3 were actually sampled

in the cores and quadrats (Table 3). *Halodule wrightii* was the most commonly encountered species, followed by *R. maritima*. *Thalassia testudinum* was observed at just 2 stations in the central region. *Syringodium filiforme* and *Halophila engelmannii* were observed in the sampling vicinity, but did not occur in any of the quadrats or cores.

Of the 21 stations sampled, 17 were monospecific and 4 were mixed seagrass species stations with the co-occurrence of *H. wrightii* and *R. maritima*. Mixed species stations were observed in both the central and southern regions. Average seagrass cover (all species combined) was 58 \pm 21(SE)% in the southern region, 81 \pm 14% in the central region, and 78 \pm 9% in the northern region. *H. wrightii* densities ranged from 2000 shoots m⁻² in the southern region to 9100 shoots m⁻² in the central region. *R. maritima* densities ranged from 1670 shoots m⁻² in the southern region to 3000 shoots m⁻² in the central region. No *R. maritima* was observed in the northern region. *T. testudinum* densities were 738 and 909 shoots m⁻² at 2 stations in the central region.

Table 3. Post exposure (August/September 2010) characterization of the seagrass species community composition, water depth, and number of stations sampled with each species in the Chandeleur Islands, Louisiana. The stations were stratified into 3 preliminary oil exposure categories based on shoreline oiling data (assessed by the Shoreline Cleanup Assessment Technique): heavily oiled (southern region), moderately oiled (central region), and no oil (northern region). N = number of stations. Values below each species indicate the number of cores in which the species was present

Sampling location	N	Mean depth (m)	<i>Thalassia testudinum</i>	<i>Halodule wrightii</i>	<i>Syringodium filiforme</i>	<i>Ruppia maritima</i>
Southern	8	0.47	0	7	0	3
Central	9	0.42	2	6	0	3
Northern	4	1.1	0	4	0	0

June 2011

In June 2011, we limited our sampling sites to the central and southern regions of the islands, but obtained a wider spatial scope of samples that included inshore, mid-shelf, and outer shelf stations (Fig. 2b,c). As was the case in our first survey, the spatial distribution of seagrasses on the shelf was a mosaic of patches distributed in varying sizes among areas of unvegetated bottom. Four seagrass species were observed and quantitatively documented. The majority (61%) of the cores had just 1 species present, but multispecies meadows were also common (Fig. 6a). At least a third of the stations were comprised of 2-species meadows, consisting of different combinations of *H. wrightii*, *R. maritima*, *T. testudinum*, and *S. filiforme*. Overall, *R. maritima* was the most frequently encountered species, followed in order by *H. wrightii*, *T. testudinum*, and *S. filiforme* (Fig. 6b).

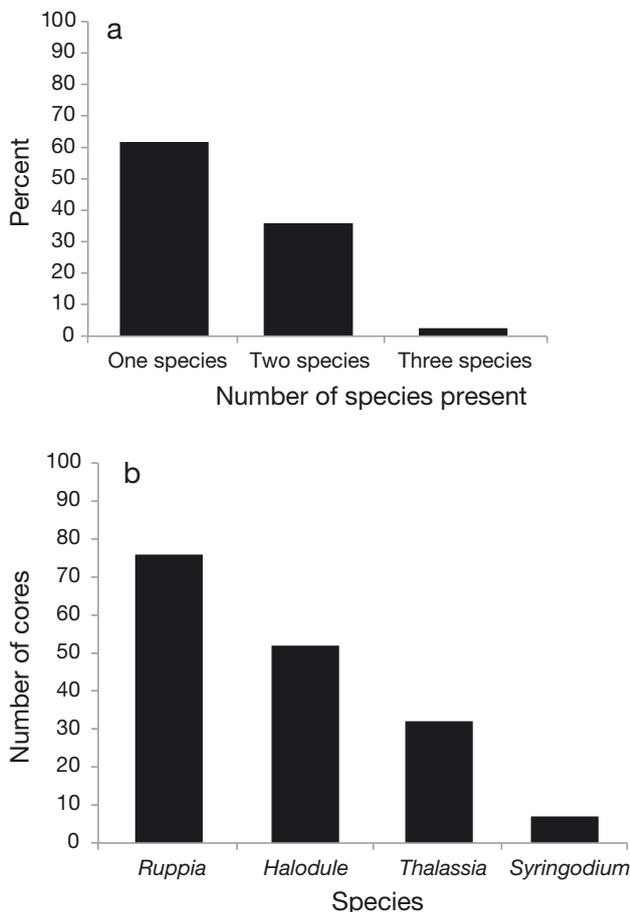


Fig. 6. (a) Percent of total cores having 1, 2, or 3 seagrass species present and (b) number of cores having each individual sea-grass species in the central and southern regions of the Chandeleur Islands in June 2011

There was some variability in the overall species abundance between the 2 regions. In the southern region, *H. wrightii* and *R. maritima* each occurred at 11 of the 14 stations sampled. *H. wrightii* was more frequently observed in the cores than any of the other 3 species (Fig. 7a). *R. maritima* was the next most frequently encountered species. *T. testudinum* was found at 5 of the 14 stations and was the next most frequently encountered species. *S. filiforme* was the least abundant species and was observed at only 1 station. Where seagrasses occurred, total seagrass cover in the southern region ranged from 72 to 100%, averaging $92.2 \pm 5\%$ and was heavily influenced by a higher abundance of *R. maritima* compared to sampling in August/September 2010.

In the central region of the islands, *R. maritima* was observed at 9 of the 10 stations and was the most frequently encountered species (Fig. 7b). *T. testudinum* was the next most frequently encountered species and was present at 5 of the 10 stations, while *H. wrightii* was less abundant than *T. testudinum* and present at 3 of the 10 stations. As in the southern

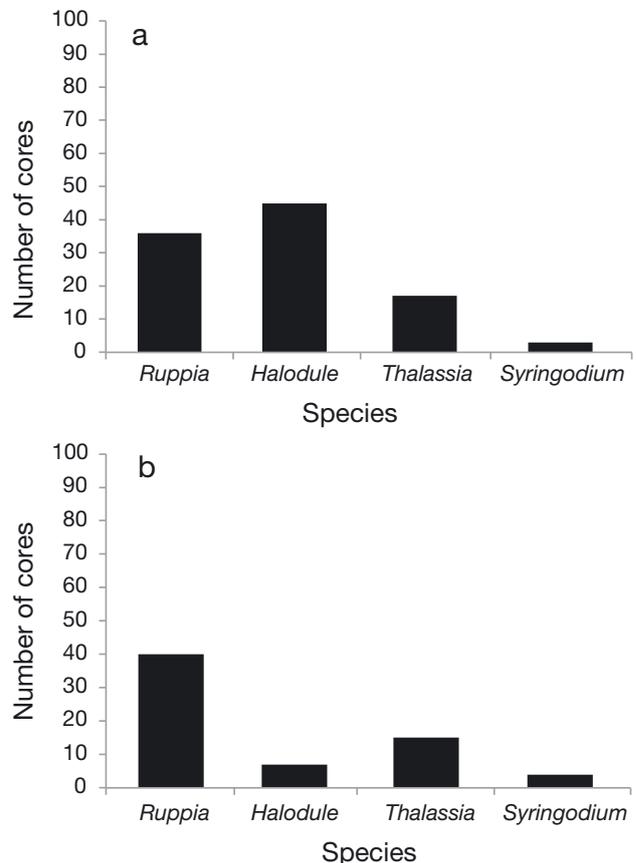


Fig. 7. Frequency of sample cores in which each species occurred in the (a) southern and (b) central regions of the Chandeleur Islands in June 2011

region, *S. filiforme* was the least abundant species. Total seagrass cover in the central region ranged from 45 to 100%, averaging $90.2 \pm 7.5\%$.

R. maritima densities were lower in the southern region (1195 ± 308 shoots m^{-2}) than in the central region (2654 ± 385 shoots m^{-2} ; Fig. 8a). Additional density data obtained in this region in June 2011 (1613 ± 509 shoots m^{-2} ; K. Heck unpubl. data) were slightly lower than our samples. Average pre-exposure densities in the central region for *R. maritima* (2872 ± 2159 shoots m^{-2}), obtained between 2006 and 2010 (Fodrie & Heck 2011), were comparable to our June 2011 densities, but had a large standard error, suggesting considerable spatial and/or inter-annual variation.

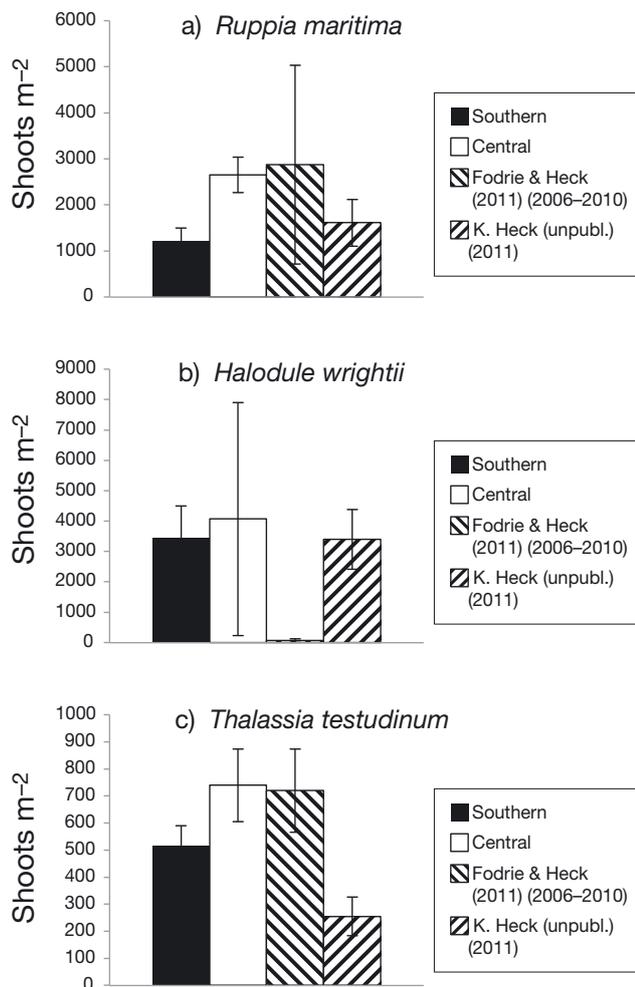


Fig. 8. Shoot density (shoots m^{-2}) in the southern and central regions of the Chandeleur Islands in June 2011 for (a) *Ruppia maritima*, (b) *Halodule wrightii*, and (c) *Thalassia testudinum*. Also shown are average shoot densities for the central region between 2006 and 2010 (Fodrie & Heck 2011) and 2011 (K. Heck unpubl. data). Error bars indicate SE

H. wrightii densities ranged from 3451 ± 1044 shoots m^{-2} in the southern region to 4067 ± 3840 shoots m^{-2} in the central region (Fig. 8b). Additional density data (3400 ± 988 shoots m^{-2}), obtained in the central region in June 2011 (K. Heck unpubl. data), were comparable to our densities. Average pre-exposure *H. wrightii* densities (68 ± 59 shoots m^{-2}) in the central region between 2006 and 2010 (Fodrie & Heck 2011) were much lower than our June 2011 samples (Fig. 8).

T. testudinum densities ranged from 518 ± 72 shoots m^{-2} in the southern region to 739 ± 134 shoots m^{-2} in the central region (Fig. 8c). Additional density data (255 ± 154 shoots m^{-2}), obtained in the central region in June 2011 (K. Heck unpubl. data), were lower than our densities in June 2011. Average pre-exposure densities in the central region for *T. testudinum* (720 ± 154 shoots m^{-2}) obtained between 2006 and 2010 (Fodrie & Heck 2011) were comparable to our June 2011 samples.

S. filiforme was present at only 2 stations, with 1775 shoots m^{-2} in the central region and 1003 shoots m^{-2} in the southern region. These densities were higher than average pre-exposure samples taken between 2006 and 2010 (358 ± 323 shoots m^{-2} ; Fodrie & Heck 2011) and samples obtained in the moderate strata in June 2011 (738 ± 237 shoots m^{-2} ; K. Heck unpubl. data).

Seagrass change detection

The first phase of the change detection along the full length of the island between fall 2010 and 2011 detected 483 acres (195.46 ha) of SAV loss and 711 acres (287.73 ha) gained, for a net positive change of 228 acres (92.27 ha). The second phase identified changes between 2010, 2011, and 2012 in the 5 AOCs (Table 4; also see Supplement 2).

Core areas were delineated to omit areas of natural processes that might be responsible for losses. For ex-

Table 4. Summary of changes in seagrass acreage in the 5 core areas in each change class category

Core area	No change	Gain	Loss	Net loss	Net gain
1	46.35	11.0	54.9	43.9	0
2	208.26	35.87	64.44	28.57	0
3	178.28	38.98	36.61	0	2.37
4	178.33	20.99	47.54	26.55	0
5	316.28	60.13	67.7	7.57	0
Total		166.97	271.19	106.59	2.37

ample, the core area within AOC 1 eliminates the overwash fans that were visible in the underlying 2012 post-Hurricane Isaac imagery. These fans resulted when waters washed over the island during the hurricane, depositing fans of sediment on the western side of the island and burying existing seagrass. The northern half of AOC 1 was also excluded, because this part of the island offered little physical protection to erosion and overwash burial, and the seagrass beds in this area had been experiencing serious losses prior to 2010. Subsequently, all 5 AOCs were analyzed to omit areas of natural loss (Supplement 2).

Despite evidence of oil exposure and both persistent and delayed losses, all of the core areas had some seagrass coverage that displayed no change or gains (see Supplement 4). Four of the 5 core areas displayed a net loss, while only 1 (core area 3) displayed a small net gain (2.37 acres, 0.959 ha). A total of 111.7 acres (45.20 ha) were identified as persistent loss and 159.5 acres (64.55 ha) were classified as delayed loss (see Supplement 4). Therefore the total loss (persistent + delayed loss) for all 5 core areas was estimated to be 271.19 acres (109.75 ha; Supplement 4). Accounting for the gains (2.37 acres, 0.959 ha), overall there was a net loss of 104.22 acres (42.18 ha) in the 5 core areas.

DISCUSSION

Deepwater Horizon oil exposure

The spatial and temporal signature of surface oil in aerial photography and SAR data clearly indicated that the spill threatened seagrass meadows located at the Chandeleur Islands, LA. Forensic analyses confirmed that some of the *Deepwater Horizon* oil was transported in surface waters shoreward into shallow coastal regions throughout the northern GoM, where it was dispersed as floating oil slicks, sheens, emulsions, submerged mats, tar balls, or dissolved in water in the Chandeleur Islands (Stout et al. 2016). Five lines of evidence presented in this study, viz. (1) shoreline oiling (SCAT data), (2) sediment and plant PAH data on 2 sampling dates, (3) concurrent forensic confirmation of *Deepwater Horizon* oil exposure (Stout et al. 2016), (4) visual inspection of oil on water in aerial photography, and (5) estimated oil on water days based on satellite imagery (SAR data), confirmed the exposure of seagrass meadows in the Chandeleurs to *Deepwater Horizon* oil.

The shoreline SCAT data confirmed what was evident from aerial photography; oil had to pass over

and through the shallow shelf and seagrass meadows west of the islands to reach the shoreline. Sediments and plant tissues showed increasing concentrations of tPAHs and petrogenic PAHs forensically matched with *Deepwater Horizon* oil between early June and September 2010 corresponding with repeated oiling events that took place over the 87 d between April and July before the *Deepwater Horizon* well was capped. By June 2011, approximately 1 yr after exposure commenced, forensic analysis continued to detect *Deepwater Horizon* oil, but tPAH and petrogenic PAH concentrations had declined markedly to values only slightly higher than initially recorded in June 2010, indicating that persistent exposure was mitigated by further redistribution, weathering, biogeochemical processing, and degradation of the oil.

Exposure scenario and seagrass response

The potential susceptibility of the Chandeleur Islands' seagrasses to *Deepwater Horizon* oil exposure is attributed to several factors. These seagrass meadows were only 125 km from the *Deepwater Horizon* source, and because of their north-south orientation, the islands provided minimal physical protection from the oil, which had a direct pathway into the seagrass meadows on the shallow back barrier shelf (Supplement 5 at www.int-res.com/articles/suppl/m576p145_supp.pdf). As oil was transported onto the shelf and ashore from the south and west, the islands acted as a barrier preventing the easterly transport of oil off the shelf. With a relatively small amount of tidal and wind energy to physically transport it away, it is likely that oil was temporarily concentrated on the shallow shelf and contacted the seagrasses directly in soluble and insoluble forms and became adsorbed onto suspended materials (sediments, detritus) and biota (epiphytes) that may have settled to the bottom and further exposed the seagrass and sediments to potentially toxic concentrations of petrochemicals (Supplement 1). The very high concentrations of *Deepwater Horizon* PAHs and petrogenic PAHs in the external materials loosely adhered to the leaves (epiphytes) suggest that this exposure could have affected the epiphyte community, thereby impacting a productive and important trophic component of the system.

Additionally, tar balls were commonly encountered during sampling, and oil that was stranded along the shoreline and in shallow subtidal sediments (Stout et al. 2016, Rouhani et al. 2017, this Theme Section) may have been redistributed back onto the inter-

tidal and subtidal shelf by wave turbulence and tidal energy leading to prolonged exposure. Subtidal, shoreline, and fringing marsh sediments and particulate detritus exposed to oiling are less cohesive than unoiled material, which may have provided a mechanism for repeated oiling of the seagrass meadows long after the well was capped (Silliman et al. 2012, Martin et al. 2015). Additionally, oiled sediments are not nearly as cohesive, and if the roots and rhizomes were impaired by exposure, seagrasses may have been more easily uprooted. This may be a partial explanation of the unvegetated gaps in substrates and water depths that normally would support seagrass.

Two field assessments and 3 consecutive years of high-resolution aerial photography confirmed that the spatial coverage of seagrasses was heterogeneously distributed across the shallow shelf west of the Chandeleur Islands. The shelf seascape was a mosaic of healthy and actively growing seagrasses in varying sized patches and large continuous meadows distributed among unvegetated and sparsely vegetated gaps. Where the seagrasses occurred, the species composition, cover, and density were comparable to seagrass meadows previously described for this region of the northern GoM (Eleuterius 1987, Green & Short 2003, Byron & Heck 2006, Handley et al. 2007, Carter et al. 2011, Fodrie & Heck 2011, Pham et al. 2014). In September 2010, monospecific species communities were more common than multi-species meadows, while in June 2011, multi-species meadows were more frequent with a demonstrably larger presence of *R. maritima*. Some of this variability in species composition can be attributed to differences in the time of sampling, as well as differences in the spatial extent of our 2 sampling efforts. In September 2010, sampling focused almost exclusively on nearshore sites adjacent to the islands, while in June 2011 the survey area expanded to mid-shelf and outer-shelf sites which captured more of the spatial variation in depth, species distribution, and community composition. Based on our 2 surveys, it is evident that some portions of a diverse and structurally complex seagrass community were exposed to MC252 oil for several months between May and August 2010, and some exposure persisted into 2011, while some areas avoided exposure.

In both sampling events, *Ruppia maritima* and *Halodule wrightii* were the most commonly encountered species in high densities throughout the shelf, in both the subtidal and shallow intertidal where leaf canopies reached the water surface and would have been most vulnerable to oil exposure. We also ob-

served *Halodule* and *Ruppia* in nearshore environments adjacent to shorelines with visibly evident accumulations of stranded oil. *Ruppia* frequently co-occurred with *Thalassia testudinum* and was relatively more abundant in the June 2011 samples, which may be indicative of seasonal differences in phenology and growth. *Ruppia* is a euryhaline, relatively fast-growing, opportunistic, and ephemeral species known to flower prolifically and colonize unvegetated areas by seed, while completing its entire life cycle in 4 mo (Moffler & Durako 1987, Dunton 1990, Byron & Heck 2006). *Ruppia* is among the most fecund seagrasses in the northern GoM and relies on rapid vegetative growth, flowering, and seed production in late spring and early summer to replenish biomass and populations. A recent experimental study demonstrated that high sediment oil concentrations impaired the production of inflorescences, fruiting bodies, and root growth of *R. maritima* (Martin et al. 2015). In June 2011, *Ruppia* flowering plants were commonly observed and widely distributed, with canopies occupying the entire water column up to the surface. If the conditions observed in June 2011 represented the conditions in May and June 2010 when oil first reached the Chandeleurs, *Ruppia* would have been especially vulnerable to exposure. The 3 other species also flower and produce seeds, and *H. wrightii* and *Syringodium filiforme* produce seeds that can be buried in sediment seed banks longer than 12 mo before germinating (McMillan 1991, Inglis 1999, Orth et al. 2006a). Flowering and seed production are important for both meadow maintenance and spatial dispersal of seagrasses (Kendrick et al. 2012), and it is likely that sexual reproduction of these species was also affected by *Deepwater Horizon* oil in 2010. Given that oil exposure was detected in sediments for at least 1 yr, it is plausible to conclude that some of the plants and sediment seed banks were chronically exposed, potentially leading to population-level impacts on the seagrasses.

The Chandeleur Islands have experienced a long history of physical instability resulting from severe storms which have reduced the overall physical size and elevation of the islands (Lavoie 2009, Mitchell et al. 2011). These storm effects and changes in water quality, mainly salinity and turbidity, have corresponded with the diminished areal abundance of seagrasses in the region (Eleuterius 1987, Poirrier & Franze 2001, Franze 2002, Poirrier & Handley 2007, Lavoie 2009, Pham et al. 2014). Unexpectedly, our change analysis identified a shelf-wide net gain of 228 acres (92.27 ha) of seagrass coverage between

fall 2010 and fall 2011. This gain is notable because it signals a pause in the long-standing persistent downward trend in total seagrass coverage in the Chandeleurs and suggests that predictions for the demise of this resource may need re-evaluation. These results, combined with the high density, cover, and observed biodiversity, provide reasonable assurance that there has been no widespread catastrophic loss of seagrasses associated with oil exposure in the Chandeleur Islands.

There was, however, a conspicuous widespread distribution of unvegetated and sparsely vegetated gaps in the cover of seagrasses at water depths and in sediment types known to support their growth. Gaps among healthy seagrass meadows are not uncommon (e.g. caused by bioturbation, grazing, or physical disturbance; Uhrin et al. 2011). However, some of the gaps we observed in September 2010 and again in June 2011 corresponded with areas of documented oil exposure, and the persistence or expansion of these gaps and the formation of new gaps were considered indications of seagrass response to exposure. We also suspected that the 3 mo delay in sampling after initial oiling prevented us from directly observing and documenting visible oil entrained and accumulated in the seagrass beds, the highest concentrations of oil the seagrass and sediments may have experienced, and the most acute and potentially severe toxic effects of exposure.

The cumulative lines of exposure evidence all indicated that oiling and the degree of exposure were spatially and temporarily heterogeneous. This variability in exposure limited our scope of inferences with point samples alone. We were also handicapped by the absence of quantitative baseline data for seagrasses at the time of exposure, thus eliminating a statistically robust before and after sampling design. To overcome these limitations, we completed our assessment using high-resolution aerial imagery and quantitative change analysis of seagrass areal distribution. Without reliable pre-exposure imagery, October 2010 served as the starting reference point for seagrass coverage and the possible latent effects of exposure that may have lingered in the ecosystem for up to 2 yr. Our change detection method in the AOCs, where we documented exposure, deviated from traditional approaches which interpret areal seagrass coverage to calculate an absolute change in area between 2 time intervals. Often, the factors potentially responsible for the change in coverage are assumed to be homogeneously distributed, in which case the net gain in seagrass areal coverage documented between 2010 and 2011 would suggest

that oiling had no effect on total seagrass abundance in the Chandeleur Islands. However, this would disregard evidence that oil exposure was heterogeneously distributed in space over a period of several months, and also overlooks the fact that seagrasses were heterogeneously distributed in such a way that the specific locations where oil reached the shelf may or may not have directly contacted the plant canopies and sediments. This alternative approach acknowledged that there could be areas of seagrass loss due to exposure and areas of no change or gain that were minimally exposed or not exposed at all. Furthermore, documenting all 3 categories over time (3 yr) acknowledges the potential latent chronic effects of exposure which were not immediately evident in field sampling following the initial exposure.

Accounting for gains, the change analysis in the 5 core areas estimated a net loss of 104.22 acres (42.18 ha). To minimize uncertainty and strengthen inferences regarding exposure, areas where changes in seagrass coverage could be attributed to natural processes and problematic interpretation signatures were excluded from this analysis. Therefore, it is plausible to attribute the net losses to acute and chronic exposure of critical plant physiological processes leading to seagrass mortality, the impairment of seagrass reproduction (sexual and/or asexual) recruitment and recolonization, and the latent effects of oil exposure on sediment biogeochemical processes. Since the imagery used in this analysis was acquired in October 2010, almost 5 mo after oil first reached the Chandeleurs, this estimate did not capture seagrass changes that might have occurred during and immediately after exposure in the late spring and summer of 2010. Thus, these estimates likely represent a conservative assessment of changes due to exposure.

SUMMARY

In the summer of 2010, the biophysical conditions on the back barrier shelf at the Chandeleur Islands were favorable to oiling from the DWH spill. Multiple lines of evidence confirmed *Deepwater Horizon* oil exposure on shorelines, in seagrass tissue, and in sub-tidal and intertidal sediments on the shelf. Given the known mechanisms linking petroleum toxicity to both lethal and sublethal impairment of seagrass physiology and sediment metabolism, we investigated the seagrass response to *Deepwater Horizon* oil exposure at the Chandeleur Islands. Despite evi-

dence of widespread oiling on the shoreline, a shelf-wide change analysis conducted between October 2010 and 2011 showed a small increase in seagrass acreage. Additional change analyses were spatially constrained to a sub-set of 5 areas where we documented exposure by 3 independent methods (aerial photography, *in situ* tissue and sediment samples, and satellite remote sensing) and accounted for natural variation and interpretation errors. By restricting our analysis to these 5 locations, we conclude that it is plausible that seagrass losses in these 5 study areas could be attributed to MC252 oil exposure. The apparent discrepancy between shelfwide gains and losses in the 5 areas we sub-sampled may be explained by the very nature of the spill that resulted in a complicated oiling scenario with temporally and spatially heterogeneous exposure. The release of oil from the well lasted for 87 d, and it arrived at the Chandeleurs after variable degrees of treatment and weathering, at different times, during different water level and wind conditions, and at different stages in the life histories of the seagrass species.

Having avoided a shelf-wide catastrophic loss of seagrass due to oil exposure, the Chandeleur Islands continue to support a diverse and extensive habitat of mixed-species seagrass communities providing important and economically valuable ecological services, one of which is physical stabilization of the shallow back barrier shelf that forms the submerged foundation which the westerly migrating barrier depends on to maintain its somewhat tenuous elevation above sea level. Sediments accreting on the shelf are trapped and stabilized by the seagrasses which also help preserve the physical integrity of the back barrier marsh by protecting the emergent wetland fringe from wind wave energy. Thus, seagrasses function to delay the predicted transition of the emergent islands to submerged shoals similar to what has occurred farther south in the Chandeleurs (Lavoie 2009). The notable pause in the shelf-wide decline indicates that recent predictions suggesting the impending extirpation of this unique and important seagrass system needs some reconsideration. Data on the spatial distribution, species composition, and abundance of seagrasses provided by this study can be utilized by scientists and resource managers as a quantitative contemporary baseline for (1) designing and implementing future monitoring programs, (2) developing resource management and restoration plans for the islands, and (3) contemplating future actions in response to natural disturbances and/or anthropogenic disasters in the region.

Acknowledgements. This study was conducted within the *Deepwater Horizon* NRDA investigation, which was cooperatively conducted by NOAA, Federal (DOI) and State Trustee (LA, MS, AL, FL) natural resource agencies, NOAA contractors, and BP. The scientific results and conclusion of this publication, as well as any views or opinions expressed herein, are those of the authors only. The authors declare no competing financial interest in the publication of this study. Funding for the study was provided by NOAA through Industrial Economics, Corp. (Cambridge, MA) as part of the NRDA process. For field and laboratory assistance, special thanks to: Newfields LLC staff; Meg Goecker, Sustainable Ecosystem LLC; Sean Meehan, NOAA; Shay Viehman, Jenny Vander Pluym, and Don Field, CCFHR, NCCOS, NOAA; and Dr. Kenneth Heck and staff, Dauphin Island Sea Lab. We also thank Ruth Spell, Jonathan Nicholas, and Colin Sutherland, as well as Tatiana Manidis from Newfields LLC for assistance with the object-based image classification, GIS expertise, figure preparation, and document editing, and Catherine Lockwood with CNL World for editing the technical report.

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Editorial responsibility: Just Cebrian,
Dauphin Island, Alabama, USA

Submitted: February 8, 2016; Accepted: November 13, 2016
Proofs received from author(s): January 23, 2017